

(Natural History), the American Museum of Natural History, the National Museum of New Zealand and the Vienna Museum of Natural History for access to specimens in their care.

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A re-analysis of *Butorides*

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Payne (1974) examined a massive series of specimens of the *Butorides striatus* complex that included 837 New World specimens, of which 72 were from Panama; these were assembled from the collections of the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), the University of Michigan Museum of Zoology (UMMZ) and the National Museum of Natural History (USNM). From this study emerged the analysis by Payne (1974), in which he developed a hybrid index for neck colour, the single variable that appeared to separate *B. virescens* (Linnaeus, 1758) from *B. striatus* (Linnaeus, 1758). Because of the intermediate nature of specimens from Panama and the southern Lesser Antilles, Payne recommended that the two taxa be lumped into a single species, *B. striatus*, as reflected by his treatment in Peters (1979: 219–226) in which he considered the complex as a single species, *Ardeola striata*.

Payne (1974: 82) based his taxonomic conclusions on specimens that he ranked by comparison with a hybrid index established from a series

TABLE 1
Hybrid index of voucher specimens listed by Payne (1974: 82)

Hybrid index (category)	Specimen catalogue number (USNM)	Colour index (as described by Payne 1974)	Specimen locality (Panama, unless country given in square brackets)
1	263848	grey	Culata [Venezuela]
2	423096	grey, tinge brown	Charco del Toro, Panamá prov.
3	444948	grey, wash brown	Rio Indio, Chilar, Colón
4	400113	brownish grey	Pesé, Herrera
5	448634	greyish brown	La Jagua, Chico, Panamá prov.
6	368472	greyish red-brown	Puerto López, Guajira [Colombia]
7	206343	reddish brown	Rio Indio, Colón
8	316840	purplish brown	Cocos Island [Costa Rica]
9	468699	dark purplish brown	Almirante, Bocas del Toro

of nine specimens (hereafter termed "voucher specimens") in the USNM. These specimens, each with its hybrid index (hereafter termed "category"), USNM number, neck colour, and locality, are listed in Table 1.

Although Payne (*op. cit.*) reported that he excluded specimens that had not completed most or all their postjuvénal molt, two of the voucher specimens (5 and 6), as well as some of the other specimens he listed in his tables, are whitish below as in the typical juvenal plumage. The brownish feathers of the tibia of these two voucher specimens are marked with indistinct blackish horizontal 'bars', a condition found in all white-bellied juvenal *virescens*. Voucher specimen 6 also resembles many juveniles of *virescens* in its more orange (less reddish) neck and cheeks; although Payne (1974: 81) indicated that the voucher specimens formed a "smoothly graded series ranging from grey through brown and maroon", the series is clearly interrupted by the colour in voucher specimen 6. The chestnut colour of this specimen extends from the tip of the feather barbs to the shaft, as is the case in adults (and voucher specimens) in categories 7–9. The variation in the brownish colour of specimens 2–5 is unrelated to intensity or shade but is dependent primarily upon the number of brownish barbs on an otherwise greyish neck; furthermore, the brownish colour of the barbs does not extend to the shaft in these specimens.

Payne (1974: 85) believed that the identity of birds in categories 4–6 would be arbitrary, but we conclude that there is a definite break between voucher specimens 5 and 6. The colour of the neck in categories 1–5 is basically grey, with the amount of brownish wash increasing as the scale increases (from "grey" to "greyish brown" in Payne's chart). On the other hand, the neck in categories 6–9 ranges from rufous to dark purplish, with no outward evidence of grey.

In western Panama (west of the Canal Zone), the neck colour generally varies from 6 to 9 in the index; specimens from eastern Panama vary in degrees of brownish wash that range from 2 to 5. Exceptions to this are one specimen from Coclé (category 6) and four from Darién (category 8).

These specimens were collected within the wintering dates (Wetmore 1965) and are probably vagrants. Birds from central Panama, with consistently higher amounts of brownish wash (mostly 3–5), were named as a subspecies, *Butorides striatus patens* Griscom, 1929, but this name is now generally synonymized with *striatus*.

It is frequently mentioned (e.g. Payne 1974: 84) that South American birds sometimes have a varying amount of brownish neck wash; indeed, an examination of other *striatus* at the USNM revealed several with a category 4 rating from Colombia and Venezuela, with scattered individuals of this ranking as far south as Paraguay (no. 390676). This does not seem abnormal, simply a reflection of normal variation in the species, which in typical South American *striatus* ranges from 1 to 4, with the greatest majority 1–3 and but a few at 4 at the brownish-grey end of the spectrum. Following this logic geographically to the north, by the time Panama is reached (excluding Darién), the range of variation has shifted slightly to 2–5, with but a few in category 5. We are somewhat puzzled by the discrepancy between Payne's chart on p. 83 (his Figure I), in which the entire sample of 72 Panamanian birds shows 14 '5s' and no '4s', and his chart of p. 84 (Figure II), which indicates 11 '4s', 5 '5s', and one '4–5'. Regardless of the judgment of 4 or 5, the fact remains that Panamanian *striatus* score 2–5, a range of variability equivalent to American *striatus* in South America except shifted up one level in the index; the two '1s' Payne shows from Canal Zone (we noted one only from Colón) were undoubtedly vagrant individuals, inasmuch as *striatus* wanders north as far as Costa Rica. Because of the great overlap and the fact that the difference is primarily in the slightly increased amount of brownish wash, we agree that *patens* is not worthy of subspecific recognition. But we wish to make it clear that we believe '*patens*' not to be a highly variable intermediate population but rather one in which the range of variation is comparable to that found elsewhere in the species; thus the "approach" in colour to *virescens* may be coincidental and part of normal geographic variability rather than an indicator of genetic introgression.

Turning our attention now to '*virescens*' (categories 6–9), we find that specimens from Bocas del Toro are typical *virescens* (categories 7–9), representing both the resident Middle American form (sometimes called *B. v. maculatus* (Boddaert, 1783)) and the migrant North American one (typical *virescens*); these forms are lumped by Payne and are indeed virtually indistinguishable. Typical *virescens* then occurs south to northwestern Panama; the species reappears as '*B. v. margaritophilus* Oberholser, 1912' in the Pearl Islands (categories 7–8), a form also properly merged with typical *virescens*. Records from farther south in Panama and northern South America (range 7–9) are all from the nonbreeding season and undoubtedly represent wintering or vagrant individuals.

Specimens in category 6 might be regarded (and indeed have been) as showing introgression. Payne does not record a single 6 from Panama in his chart on p. 84 and listed but two out of his total of 72 on p. 83; we found but a single Panamanian bird (collected in early March in Coclé) that could be graded a 6. It appears to be a typical *virescens* with a lighter shade of rufous-brown on the neck; the bird does not appear to be intermediate

between *virescens* and *striatus*, being much more like typical *virescens*. We point out also that the lighter shade of rufous-brown is typical of Lesser Antillean birds. Although we did not do an extensive analysis of Antillean birds, it is our opinion that this Panamanian individual as well as the Colombian bird that Payne used as the voucher specimen for 6 in the index are either vagrants from the Lesser Antillean populations or else extreme variants of typical *virescens*, more likely the former.

It has been suggested that introgression is extensive in the southern Caribbean region, as evidenced by the large number of 5s and 6s (see Payne's chart, p. 83), but if introgression occurs there, it is at a very low level. Recently, Voous (1986, and pers. comm.) has determined that any 'intermediates' in the area of close approach or possible overlap in the southern Lesser Antilles amount to no more than 6% of the population. It seems likely that even this low percentage may be based on vagrant *B. striatus* (category 5). In any case, there is no evidence of significant introgression in the Lesser Antilles. *B. striatus* is also the resident form on Trinidad, whereas it is *B. virescens* on Tobago and the Lesser Antilles to the north. Of great interest in all this is that not once, in Panama or the Antilles, has a mixed breeding pair ever been reported.

Based on this analysis, we feel that there is no substantial evidence that there is interbreeding, and certainly if it occurs at all, it must be at a low level. Thus *B. virescens* (Green Heron) and *B. striatus* (Striated Heron) should be regarded as separate species unless there is strong new evidence to the contrary.

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APPENDIX

Other Panamanian specimens, arranged by hybrid index, as determined by the authors—total 49, including voucher specimens: 28 *virescens* (indices 6–9), 21 *striatus* (indices 1–5).

Hybrid index (category)	Specimen catalogue number (USNM)	Specimen locality
1	385963	Jaqué, Darién
1	385964	Jaqué, Darién
1	444949	Rio Indio, Chilar, Colón
2	469773	Mouth of Río Paya, Darién
2	385961	Jaqué, Darién
2	385962	Jaqué, Darién
2	448635	La Jagua, Chico, Panamá prov.
2	533940	nr. Gatun Locks, Canal Zone
3	444947	Rio Indio, Chilar, Colón
3	400111	El Barrero, Herrera
4	476623	Las Palentas, Los Santos
4	460544	Juan Mina, Canal Zone
4	400112	El Rincón, Herrera
4	389642	Río Jaqué, Darién
5	460546	Juan Mina, Canal Zone
5	400109	Santa María, Herrera
6	444951	El Uracillo, Coclé
7	444950	El Uracillo, Coclé
7	206342	Río Caña Quebrado, [state?]
7	460541	Isla Coiba
7	460542	La Lajas, Chiriquí
7	400108	Paris, Herrera
7	400110	Santa María, Herrera
7	206340	Rio Indio, Canal Zone
7	206341	Rio Indio, Canal Zone
7	471157	Isla del Rey, Pearl Is. [<i>margaritophilus</i>]
8	376004	San José I., Pearl Is. [<i>margaritophilus</i>]
8	376005	San José I., Pearl Is. [<i>margaritophilus</i>]
8	376013	San José I., Pearl Is. [<i>margaritophilus</i>]
8	376104	San José I., Pearl Is. [<i>margaritophilus</i>]
8	200443	San Miguel I., Pearl Is. [<i>margaritophilus</i>]
8	423097	Chivrán, Panamá prov.
8	206746	Gatun, Canal Zone
8	423097	Chivrán, Panamá prov.
8	305592	near Yavisa, Darién
8	305594	near Yavisa, Darién
8	385960	Jaqué, Darién
8	206344	Rio Indio, Canal Zone
9	460540	La Lajas, Chiriquí
9	606050	Chiriquí Lagoon, Bocas del Toro